The Transplantation of Individual Rat and Guinea-pig Whisker Papillae

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WITH TWO PLATES

INTRODUCTION

PREVIOUS work on the pigmentation and transplantation of hair and skin has been performed mainly on gross skin areas (e.g. Billingham & Medawar, 1950; Ebling & Johnson, 1959; Rawles, 1955) and several studies have been concerned with the histological appearances of various stages in hair development, sometimes correlated with the effects of chemical or physical agents (e.g. Chase, 1955; Chase, Rauch & Smith, 1951). So far there have been no reports of successful transplantation of individual hair papillae, although several authors have considered this to be a possibility (e.g. Billingham, 1958). Lillie & Wang (1941, 1944) showed that a feather papilla may produce generations of feathers after transplantation to another follicle, and that the feathers produced from a transplanted papilla containing both dermal and epidermal components ('whole papilla') are of donor tract structure and colour; feathers produced from local ectoderm under the influence of a transplanted dermal papilla are of host tract structure and colour. It was considered that such an approach to the study of the epigenetic relationships involved in the growth of hair might throw some light on such problems as the precise functions of the dermal papilla, the mechanism by which hair follicles produce different kinds of hair, and the functional morphology of the hair-cycle.

Several attempts have been made to determine the relationship of the dermal papilla to hair growth. Crounse & Stengle (1959) have transplanted human 'hair roots', in Millipore chambers, to the peritoneal cavities of mice, with and without the dermal papillae. Sixteen of 28 transplants including dermal papillae survived, but all 20 deprived of their dermal papillae degenerated. It was concluded that the dermal papilla is necessary for maintenance of the organization of the 'hair root'. As a result of X-irradiation experiments Geary (1952) concluded that it is the destruction or disorganization of the dermal papilla which results in the permanent hair loss found after intense irradiation, while temporary

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epilation results from an action on the matrix (ectodermal part of the papilla). Van Scott & Ekel (1958) have correlated the number of mitoses in the matrix and its volume with the number of cells in the dermal papilla and with its volume, in normal human scalp-hair, in early male baldness, in alopecia areata, and after therapy of various kinds. They found correlations between the measurements of dermal papillae and those of the matrix, and consider these evidence of an epigenetic effect. Chase (1954) considered the dermal papilla of the hair to be an inductive agent comparable with that of the feather, and believed that the dermal papilla maintains its integrity throughout the growth-cycle.

Because of the large size of their papillae it was decided to confine experiments to the whiskers until such time as the technique had been developed sufficiently to deal with the tiny papillae of the pelage. The whisker appears to resemble a guard hair of the pelage very closely except, of course, for its size, its large perifollicular blood sinus, and its considerable innervation (Melaragno & Montagna, 1953; Vincent, 1913). An additional advantage accruing from the use of whiskers is the easy recognition of donor type hair among the hairs of the implantation site.

EXPERIMENTAL TECHNIQUE

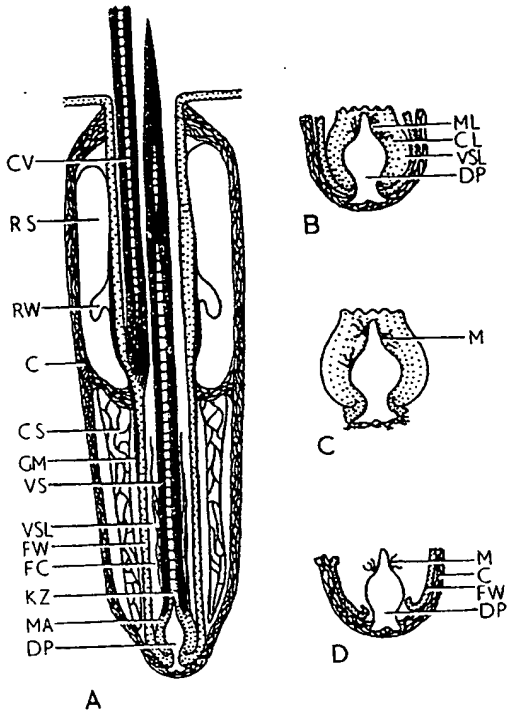
White-haired red-eyed guinea-pigs and Hooded rats were used. All transplants in these series were autografts, performed on animals anaesthetised by intracardial injection of Nembutal (Abbott), 0·055 c.c./100 g. body-weight.

As the follicle is relatively much deeper and narrower than a feather follicle, it is impractical to approach the papilla by incising down the length of the follicle as is the practice with feather follicles. Instead the inner ends of the vibrissa follicles were exposed as follows: the upper lip and the bases of the whiskers were moistened with spirit and a shallow incision about 1–1½ cm. in length was made just dorsal and parallel to the upper lip on one side. The deeper fascia was then cut parallel to the skin surface, the flap of tissue was reflected over a glass rod, and the exposed follicle bases were dissected *in situ* under a low power (×25) stereoscopic microscope, the ends of the follicles being dissected free of loose connective tissue and removed by a transverse cut. These were kept in saline until sufficient (up to 20) had been removed and then the flap was stitched back into place. Such implants will be called 'end bulbs'. The wound healed in 5–8 days, and at no time did the animals have difficulty in feeding or drinking.

These end bulbs (Plate 1, fig. B) were removed by a transverse cut across the proximal end of the perifollicular sinus. In most cases this cut passed through the apex of the papilla just proximal to the keratogenous zone (see Text-fig. 1 A, B), but considerable variation was found; in some cases part of the keratogenous zone of the whisker shaft was included, while in others the cut exposed the apex of the dermal papilla.

The end bulbs were in most cases further dissected:

(i) The whole papilla (Plate 1, fig. C; Text-fig. 1c), i.e. the dermal papilla with its ectodermal investment ('matrix'), was dissected free of adherent follicle wall and capsule by inserting one blade of a pair of extra fine iridectomy scissors into the follicular cavity and making a longitudinal incision almost to the base of the



TEXT-FIG. 1. A, diagrammatic sagittal section of whole whisker follicle (compare Plate 1, figs. A, B). B, diagrammatic sagittal section of 'whole follicle base' (compare Plate, 1, fig. B). C, diagrammatic sagittal section of 'whole papilla' (compare Plate 1, fig. C). D, diagrammatic sagittal section of first stage in obtaining dermal papilla. The ectodermal part of the papilla has been expressed from the follicle base. Some melanocytes remain on the dermal surface (Plate 1, fig. D).

C, capsule; CL, cortical layer; CS, cavernous sinus; CV, club vibrissa; DP, dermal papilla; FC, follicular cavity; FW, follicle wall; GM, glassy membrane; KZ, keratogenous zone; M, melanocytes; MA, matrix; ML, medullary layer; RS, ring sinus; RW, *ringwulst*; VS, vibrissa shaft; VSL, vibrissa sheath layer.

follicle wall. A cut round the base of the whole papilla left only a disk of capsule adherent below the dermal papilla. This was peeled off with forceps. (The term 'whole papillae' has been used for the corresponding structures in feathers, by Lillie & Wang.)

(ii) The dermal papillae (Plate 1, fig. D) were obtained by exerting gentle pressure on the sides of the end bulb with forceps; this pressure causes the dermal papilla and adherent capsule to separate from the ectodermal component of the whisker papilla—the break occurring as an annulus where the follicle wall is

reflected around the base of the dermal papilla (see Text-fig. 1D). In end bulbs which were producing pigmented whiskers, the dermal papilla so removed (Plate 1, fig. D) usually had some melanocytes around its distal surface—many of these had processes which seemed to have been drawn from between the distal ectodermal cells. Most of the melanocytes, however, remained in the ectoderm.

In addition, several whole whisker follicles were dissected out and examined histologically. These preparations were compared with dissections of end bulbs, whole and dermal papillae, and with sections of these structures (Plate 1, figs. A–D). The sections of rat and guinea-pig follicles revealed a close similarity to those of the mouse described by Melaragno & Montagna (1953) and Davidson & Hardy (1952), and confirm the anatomical observations of Vincent (1913). Text-fig. 1A illustrates the anatomy of the whole follicle, and Text-figs. 1B, C are interpretations from this sectioned material.

End bulbs, whole papillae, and dermal papillae were implanted into various sites. Initially the implantation was made into thigh skin which had been shaved and washed with spirit, but later the grafts were implanted into stomach wall, under splenic capsule, and into dorsal ear skin. In all the rats white whisker tissue was always implanted into left ear and black whisker tissue into right ear.

EXPERIMENTAL RESULTS

(*A*) *Implantation of end bulbs*

(i) Twenty-two end bulbs were implanted into shallow slits in the skin over the inner aspect of the thighs of 6 rats and 2 guinea-pigs. Biopsy at intervals of up to 24 weeks showed only degenerative changes, and no production of whisker. All appeared to have become encapsulated by 12 weeks, and later biopsies showed only the remains of the collagenous follicle sheath and fragments of keratin. No vascularization of the implants could be observed.

(ii) Six end bulbs were implanted into the stomach wall of one rat. These had similarly regressed at 14 weeks.

(iii) Acting on a suggestion by Professor H. B. Chase, that early vascularization was probably essential to such implants, 16 end bulbs were implanted under the splenic capsules of 3 rats. Two of these were killed 9 weeks after the operation and the spleens were sectioned. Of 12 end bulbs implanted, 7 were located in the sections and found to be healthy although producing no whisker. The third rat, killed at 13 weeks, had received 4 end bulbs of which 3 were located. These had produced whiskers of 0·5 mm., 1·2 mm., and 1·3 mm. in length.

(iv) Because of the difficulties inherent in the transplantation to spleen, and the impossibility of continuous observation, 14 end bulbs were transplanted to sites under the ear epidermis of 3 guinea-pigs. The ear was shaved and washed with spirit and a small nick made in the dorsum. A small scalpel blade was then inserted parallel to the surface and the pocket so formed was washed out with saline. Precise orientation of the end bulbs was impossible. At biopsy 8–12 weeks

after the operation only 6 of the end bulbs were located. Two of these had produced whisker shafts with estimated lengths 0·6 mm. and 2·8 mm. This last is illustrated in Plate 1, fig. E.

(v) Fifty-two end bulbs were then similarly transplanted into the ears of 7 rats. Six of these animals produced, over a period of 2 years, lengths of recognizable whisker above the skin surface. Many whiskers were also produced which failed to emerge but coiled in the skin and were recognized as elevated 'rings'; several of these were dissected (Plate 2, fig. J). A total of 26 emergent whiskers was produced by these implants, and at least 18 more failed to pierce the skin. This latter number is doubtful, as successive generations, lying together, could not be distinguished from each other in each 'ring'; three of the 'rings' which were dissected had in fact two separate whisker coils, and one had three. It is of interest that in one of the double 'rings' the two whiskers coiled in opposite directions although both had apparently been produced from the same implant. One rat, which had received 2 end bulbs which had previously produced black whiskers, produced the following whiskers, all from the same follicle, in the sequence shown: (*a*) A coiled black whisker with truncated tip, about 2 cm. in length. All succeeding whiskers had attenuated tips. (*b*), (*c*), (*d*), (*e*) White whiskers, apparently normal, all over 2 cm. in length; (*b*) is illustrated in Plate 2, fig. G. (*f*) Another small black whisker, definitely from the same follicle, 1·2 cm. long. (*g*) A small hair-like whisker, dark at the tip with a white shaft. The rat at this time was nearly 2 years old, and showed considerable hair-loss and depigmentation of its pelage. It died with this whisker still present and the ear was sectioned. Unfortunately this was technically unsuccessful. The follicle may be seen, but fixation distortion has resulted in considerable damage to the whisker base and the papilla. Such pigmentation changes in successive generations occurred in several series.

(*B*) *Implantation of whole papillae*

(i) One guinea-pig produced 2 successive whiskers from one follicle after 12 whole papillae had been implanted into its left ear. Four additional papillae, apparently normal but with no whisker or follicular structures, were found at biopsy. Another guinea-pig received 3 whole papillae, produced no whisker, and no implants could be found at biopsy 8 months later. A guinea-pig which had received 3 whole papillae died 6 days later. The implants had achieved a blood-supply but had produced no whisker.

(ii) Sixty-two whole papillae were implanted into the ears of 6 rats. Four of these rats produced emergent whiskers, one produced only 'rings', and one produced nothing and no traces of implants could be found at biopsy 13 months later. All whiskers were of donor-type pigmentation (13 white in left ears, 12 black in right ears) except for one, third generation in right ear, which had a black tip but a white shaft. Two second-generation white whiskers are shown

in Plate 2, fig. H. Five successive generations were produced from one follicle, all apparently normal whiskers.

There was no apparent difference in size between whiskers produced from whole papillae and from end bulbs.

Sections of rat ears in which whole papillae had been implanted and which were producing whisker, revealed that the follicles organized by the implants were of two kinds. In several cases the follicular epithelium was very thick and resembled that of the whisker follicle (Plate 2, fig. K); in most cases, however, it was thin and resembled that of local follicles (Plate 2, fig. L). In two cases it is possible to observe a discontinuity at a level in the follicle, the epithelium being much thicker (about 4 cells) proximally and thin (1–2 cells) distally. Sebaceous glands attached to thin epithelium resemble those of the local hairs, but those on the thicker-walled follicles, while not resembling those of the whisker in their position and relationship with a peripheral blood-sinus, do resemble them in that they appear to be ductless, and poorly developed in general. In no case was a peripheral blood-sinus found, nor a *ringwulst*, nor a glassy membrane. These latter observations apply also to end-bulb implants; however, all of these which were sectioned had whisker-type follicles in all other respects (Plate 2, fig. K).

(*C*) *Implantation of dermal papillae*

Sections of one rat ear which had received 11 dermal papillae, 4 weeks after the operation, revealed no necrotic or otherwise degenerate structures, but no whisker had been produced (as judged by the diameter and the character of the medullae of such hairs as were present). Several aggregations of cells in the mesoderm were tentatively identified as the implants. One of these was in contiguity with a fold of ectoderm from an adjacent follicle; unfortunately the contiguity is in the plane of the section and cannot be photographed. Two follicles in the vicinity have very short lengths of hair and no sebaceous glands, and the apices of the papillae are directed toward the cartilage and their bases toward the skin. It is perhaps equally likely that these follicles have not been organized by the implants but have been broken and re-orientated by the actual implantation procedure and subsequent reorganization of the superficial layers. Their dermal papillae are not abnormally large as compared with others near by, and are small compared with those of the whiskers.

A further two rats each received 10 dermal papillae, and neither produced any recognizable whisker in periods of 8 and 9 months after the operation. 'Inverted' follicle bases may be seen in section.

Thirteen dermal papillae, selected for large size, were implanted into a small area (about 2 sq. mm.) of the ear of another rat; the implantation site was marked with Indian ink on the surface after the scab had fallen off (3 days post operation). The rat was killed 7 days after the operation and the site sectioned. Seven dermal papillae have been located with certainty. Despite some difficulty in adequate preparation and staining of these sections it may be clearly seen that

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epidermal downgrowths have appeared which have come into relationship with the dermal papillae. Three separate downgrowths have been examined in detail. One appears to derive from the original cut edge of the incision, one from a local hair follicle cut during the incision, and one may have derived directly from the surface epidermis. (It is not clear whether this epidermis represents the original ear surface or whether the original flap died and the site was covered by growth from the margins.) Plate 2, fig. M illustrates part of one section of the site; two downgrowths may be seen, one of which has invested three implanted dermal papillae, which have been sectioned tangentially. The section was chosen as it shows the connexion with the epidermis. Plate 2, fig. N shows part of another section (80μ distant); a dermal papilla has acquired a 'matrix' from the downgrowth.

(D) Structure of whiskers produced by the implants

Those whiskers which have been produced from the implants have all been small compared with natural whiskers, and many have been more or less curled, a condition which is only found very rarely in the normal whisker. In some cases the first-generation whisker from an implant has appeared truncated at its tip, but most of these, and all whiskers of subsequent generations, have tapered to a fine tip. The rate of growth has not been measured accurately, but appears to be very much slower than whiskers growing in their own follicles. Maturity of the whiskers was attained in all but a few cases, the shed whisker having a 'club' end which compares exactly with those of naturally shed whiskers. However, at no time were two whiskers present in one 'follicle', and a period of at least a month elapsed between the shedding of one generation and the emergence of the tip of the next. Sections of the ears which had received implants and were producing whiskers suggested that the 'follicles' in which these whiskers grew were formed from both local ectoderm and donor ectoderm—this is doubtful in cases where whole papillae were implanted, where it seemed as if the entire follicle was derived from local ectoderm (see above under (*B*) (ii)). In no case could any ring sinus or capsule be distinguished. This may account for the fact that when attempts were made to dissect or pluck out these whiskers, the papilla almost invariably came out on the end of the shaft.

(E) Effect of removal of whisker bases on subsequent growth

In all cases whisker bases were dissected only from one side of the animal. A smaller number of whiskers was subsequently produced on this side, and some evidence for the belief that follicles whose papillae have been removed degenerate has been obtained by examining the site of removal at autopsy, when cords of fibrous tissue normal to the surface were found; these are not present before the operation, and may represent degenerated capsules or perhaps follicles. Their number corresponds approximately with the number of follicle end bulbs removed.

DISCUSSION

These experiments have shown conclusively that whole follicle end bulbs and isolated whole whisker papillae (containing dermal and epidermal components) remain viable and may produce whiskers in a new site. The whiskers are shed and new whisker grows from the same follicle. However, a large proportion of transplants failed. In many cases histological examination indicated not only that some of the implants had regressed, but that others had been lost entirely, presumably due to imperfections of the implantation procedure. For this reason it is considered that the low percentage of successful transplants does not necessarily reflect a low viability of the implants, but rather an inadequate preparation of the implantation sites.

The fact that several of the implants have produced more than one whisker generation must mean that it is not only that the whisker which was being produced before removal is completed, but that new cycles are initiated in the new site. The papilla must therefore retain its integrity (as does the feather papilla) and be unaffected by the reorganization of the follicle during the growth cycle. This reorganization in vibrissa follicles is by no means as dramatic as in some hair follicles, but the close relationship of the two structures makes it extremely likely that the hair papilla is also permanent in this sense.

The orientation of the whiskers produced by the implants has been completely random, and presumably derives from the orientation of the implanted papilla rather than from any local influence; this would agree with the results of Lillie and Wang on the feather.

Those experiments in which dermal papillae were implanted have demonstrated that the vibrissa dermal papilla, like the feather papilla, retains its inductive capacity and, even in the adult, may call upon local ectoderm to invest it. The new follicles organized by the implanted papillae are not recognizable among the native follicles 4 weeks after the operation (except perhaps in their orientation, which may well depend upon that of the implant). It is unlikely that they have degenerated, as none of the remains were found. It may therefore be supposed that hair and follicles of local type are produced by the local ectoderm under the influence of a vibrissa dermal papilla. The vibrissa whole papilla, on the other hand, produces hair of donor type (whiskers) and part of the follicle often appears to be of donor ectoderm. This lends support to the belief that the differences which result in the production of hair or whisker reside in the *ectoderm* concerned in the production.

The vibrissa dermal papilla is usually much larger than that of the ear hairs. However, 4 weeks after implantation such large dermal papillae cannot be found. The possibility therefore exists that (as in the work of van Scott & Ekel) an ectodermal influence on the papilla has resulted in a reduction of the volume of the dermal papilla and perhaps a corresponding reduction in the number of cells in it. Work is proceeding which will test this hypothesis.

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It is concluded that the results published here show a similarity between the epigenetic situation described for feather follicles and that found in whisker and hair follicles; the dermal papilla is a non-specific organizer throughout its history, the local specificity of plumage and probably also pelage being dependent upon intrinsic properties of the local ectoderm.

SUMMARY

1. A method is described for the removal and transplantation of vibrissa follicle bases (end bulbs).

2. The whole papilla may be dissected from the capsule and follicle wall, and the dermal papillae may also be dissected out.

3. Transplants have been made to various sites. No whisker was produced from end bulbs implanted into body skin, but whiskers were produced from end bulbs in the spleen, and from both end bulbs and whole papillae under ear skin.

4. Several generations of whisker have been produced from some of the implants, but retention of the club whisker has not been observed.

5. It is concluded that the whisker papilla is a permanent entity in the same sense as is the feather papilla, despite follicular changes during the growth-cycle.

6. Dermal papillae may cause local ear epidermis to invest them, and presumably this produces hair of local kind, as no whisker or whisker follicle was discovered.

7. It is suggested that the whisker papilla is a non-specific organizer, specificity residing in the ectoderm concerned.

RÉSUMÉ

Transplantation de papilles de vibrisses individuelles de Rat et de Cobaye

1. On décrit une méthode d'exérèse et de transplantation des follicules basaux des vibrisses (bulbes terminaux).

2. On peut disséquer la papille entière à partir de la capsule et de la paroi folliculaire, et les papilles dermiques peuvent également être extraites par dissection.

3. Les transplantations ont été faites en divers endroits. Les bulbes terminaux implantés dans la peau du corps n'ont pas produit de vibrisses, mais celles-ci se sont formées à partir de bulbes implantés dans la rate et à partir de bulbes et de papilles entières transplantés sous la peau de l'oreille.

4. Quelques implants ont donné plusieurs générations de vibrisses, mais on n'a pas observé de rétention de vibrisse à croissance achevée.

5. On conclut que la papille de la vibrisse est une entité permanente comme l'est la papille plumaire, malgré les modifications folliculaires au cours du cycle de croissance.

6. Les papilles dermiques peuvent induire l'épiderme local de l'oreille à les

revêtir, et ceci donne probablement naissance à du poil de type local, car on n'a pas observé de vibrisse ou de follicule correspondant.

7. La papille de vibrisse serait un organisateur non spécifique, la spécificité étant localisée dans l'ectoderme mis en jeu.

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EXPLANATION OF PLATES

PLATE 1

FIG. A. Longitudinal section of proximal end of Hooded rat whisker follicle, sagittal; stained Harris's haematoxylin and eosin. ×190.

FIG. B. Longitudinal section of rat follicle 'end bulb', sagittal; stained by Mallory's 1936 method. This tissue was orientated and sectioned in a plasma clot, which may be seen surrounding it. ×210.

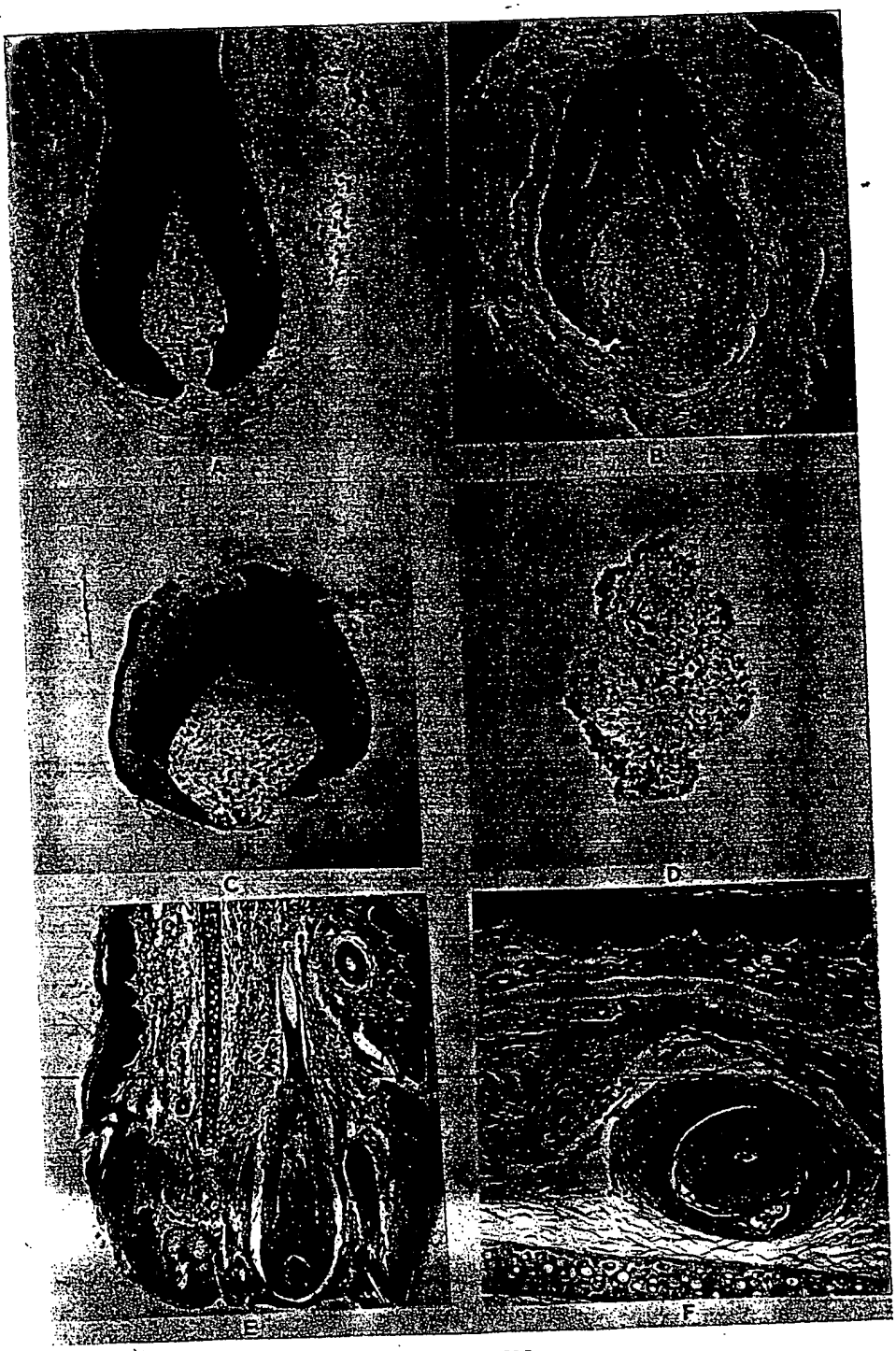

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Plate 1

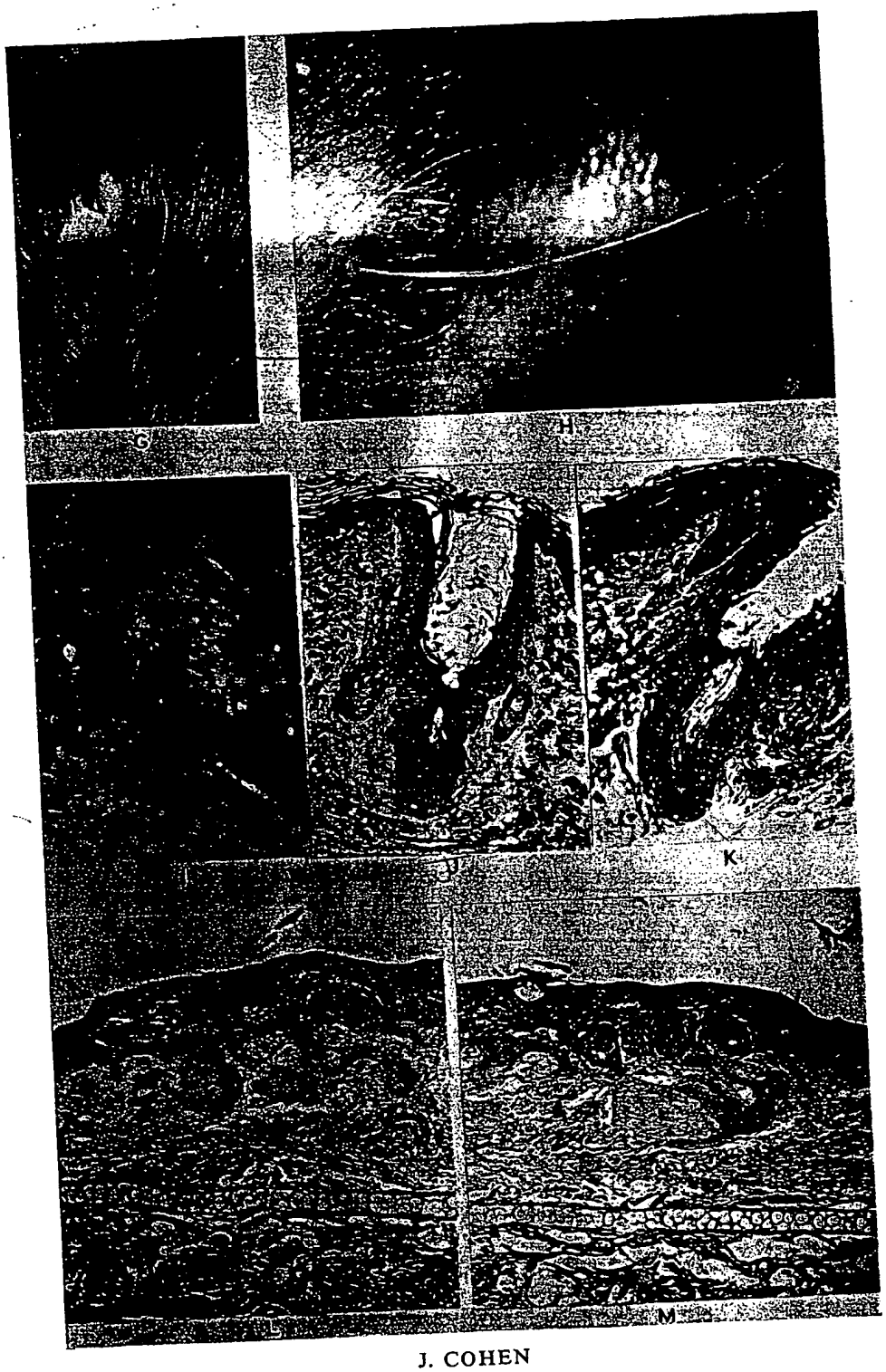

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Plate 2

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FIG. C. Longitudinal section of rat 'whole papilla', parasagittal; stained Harris's haematoxylin and eosin. The material surrounding it is gelatine, in which the papilla was orientated and sectioned. ×210.

FIG. D. Longitudinal section of a 'dermal papilla', dissected routinely from a rat-whisker follicle base, parasagittal; stained by Mallory's 1936 method. This tissue shrinks considerably in preparation. Melanocytes may be seen around the distal end. The cellular tissue at the left of the base is liver, on which it was orientated and sectioned. ×450.

FIG. E. Section of guinea-pig ear normal to surface, showing implanted whole follicle base which has produced follicular structures and a length of whisker, not all of which is in the plane of the section. Stained by Harris' haematoxylin and eosin. ×35.

FIG. F. A similar section of guinea-pig ear, with a whisker in transverse section; stained by Mallory's 1936 method. ×75.

PLATE 2

FIG. G. Right ear of Hooded Rat which has received whole follicle bases (black). The whisker shown is second generation, white, and apparently structurally normal.

FIG. H. Second generation white whiskers produced in Hooded Rat left ear which had received whole papillae (white).

FIG. J. Dissection of a 'ring' produced after implantation of 'whole papillae' (white) into the left ear of a Hooded Rat. The white whisker and its follicle may be seen.

FIG. K. Section of rat ear through the distal part of a follicle associated with an implanted end bulb and the whiskers it produced. The follicle wall is thick, like that of the distal part of the normal whisker follicle, and the sebaceous glands are typically whisker type. Stained Mallory's 1936 method. ×75.

FIG. L. Section of rat ear through the distal part of a follicle associated with an implanted whole papilla and the whiskers it produced. The follicle wall is thin like that of local follicles. A club whisker base is present. Unfortunately the section is not flat and parts are not in focus. Stained Mallory's 1936 method. ×15.

FIG. M. Section of rat ear, normal to surface, 7 days after implantation of dermal papillae. An epidermal downgrowth (from the left of the picture) may be seen to have come into association with three dermal papillae, which have been sectioned tangentially. This section was chosen despite its technical imperfections as it shows the connexion of the downgrowth with the epidermis (the original incision was to the *right* of the photograph). Stained Mallory's 1936 method. ×40.

FIG. N. Another section from the same series, 80 μ distant. Another implanted dermal papilla may be seen to have acquired a 'matrix'. ×50.

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